SOIL MICROSTRUCTURES - CONTRIBUTIONS ON SPECIFIC SOIL ORGANISMS

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Quaestiones Entomologicae
21: 497-514 1985

ABSTRACT

The soil zoological approach to the soil micromorphological studies is described. The ecological methods, e.g., *synecological analysis of soil animal communities, succession of soil animals, autecology, etc. are determined as basic methods for evaluating soil thin sections from soil-zoological point of view. The role of soil animals in formation of soil microstructure is divided into three basic categories: A) disintegration of dead organic matter, B) formation of zoogenic microstructural soil matrix, and C) tunnelling and burrowing activities of soil animals. The role of different groups of soil animals in disintegration of dead organic matter is described and the characteristic features are documented on soil thin section figures. The characteristic microstructural features of humus development during the succession are described. The short term processes of decomposition (disintegration) in humus profile relate to the long term development of humus form during the succession as does ontogeny to phylogeny in the animal kingdom in Heckel's biogenetical law. The droppings of different groups of soil animals are described from the morphological point of view and their location in the soil profile is given.*

RÉSUMÉ

L'auteur décrit la méthode pédo-zoologique d'etude de la micromorphologie des sols. Les méthodes écologiques, telles que l'analyse synécologique des communités animales des sols, la succession des animaux des sols, l'autécologie, etc., *sont considérées comme des methodés de base pour l'evaluation des coupes minces de sol d'un point de vue pédo-zoologique. Le rôle des animaux des sols dans les processus de formation de la microstructure des sols se divise en trois catégories fondamentales: A) désintégration de la matière organique morte, B) formation de la matrice microstructurale zoogénique, et C) percement de tunnels et fouissage par les animaux endogés. L'auteur décrit le rôle de différents groupes d'animaux des sols dans la désintégration de la matière organique morte et en présente les traits caractéristiques sur des figures de coupes minces de sols. Il décrit aussi les traits microstructuraux caractéristiques du développement de l'humus durant la succession. Les processus de décomposition (désintégration) à court terme ayant lieu dans la couche d'humus sont en rapport avec le développement à long terme du type d'humus au cours de la succession de la même façon due l'ontogénie l'est à la phylogénie chez les animaux, tel que le repporte la loi biogénétique d'Heckel. Finalement, l'auteur décrit les excréments de différents groupes d'animaux des sols d'un point de vue morphologique et indique leur emplacement dans le profil du sol.*

INTRODUCTION

Micromorphological methods of soil investigation were originated and developed by Kubiena as a soil biological approach to pedological problems. They were used in soil biology in the 40's and 50's by Kubiena (1943, 1948, 1955) and his collaborator Kühnelt. Primarily through the contributions of pedologists, geologists, and to a lesser extent by the soil biologists, method, theory and nomenclature of soil micromorphology were further developed in the 60's and 70's, when soil micromorphology became an independent branch of pedology. In spite of important publications using soil micromorphological methods, the number of soil biologists using these methods has been and is still very low and does not reflect their present and future importance. This international meeting of soil zoologists, soil micromorphologists and pedologists is an important step in collaboration among specialists of these ecological branches. Only by such an interdisciplinary collaboration is it possible to obtain new and untraditional views on soil and on complicated, dynamic soil processes.

Soil micromorphology has already helped to solve some practical problems in soil biology. It is possible to use it for monitoring man's impact on the environment, for solving practical questions connected with soil fertility and recultivation, for solving theoretical problems of soil development, *et cetera.*

The literature about soil micromorphology contains some contradictory results. My contribution summarises and discusses both my own and published results dealing with the role of soil animal groups in forming soil microstructures. A wider examination of these problems enables better understanding of ecological patterns in formation of microstructure and in soil development generally. For this reason my contribution also includes soil micromorphological methods from a soil zoological viewpoint. One part is devoted to the diagnosis of the tracks of soil animal activities in the soil. Some unsolved or controversial questions will also be pointed out, to stimulate work in some new directions.

My own results are from soils in the temperate, subpolar, alpine and mediterranean zones and from some subtropical and tropical soils in Cuba.

METHODS

Methods of preparing thin sections of soil and their morphometric evaluation are well described in the book edited by Jongerius (1964). Methods for evaluation of soil thin sections from the soil zoological point of view are more complicated due to the difficulty of determining the origin of the zoogenous microstructures.

To determine the zoogenous microstructural components of the soil we must start from the coenological analysis of the zooedaphon in the soil under study, from the food requirements of the dominant species of the soil meso-, macro- and megafauna, from the shape and size of faecal pellets obtained in the laboratory, from newly captured animals, and from direct observation of some dominant species in the field.

The coenological analysis of soil animal communities enable determination of the dominant species in the soil under study. In the second step we identify the predators, phytophagous and microphagous species which do not play a direct role in processes of soil microstructure formation. For questionable taxa, it is necessary to analyse the gut content to establish the roles of such species in forming the soil microstructure. It is important to point out that populations of some soil animals have synchronised food consumption and that such animals (*e.g.,* Collembola) do not feed during certain life periods (ecdysis). For such animals, it is necessary to analyse the gut content repeatedly. Some soil animals appear in high numbers only in some parts of the year (*cf.* Rusek, 1984), also important to remember in evaluating the role of such animals in the soil forming processes.

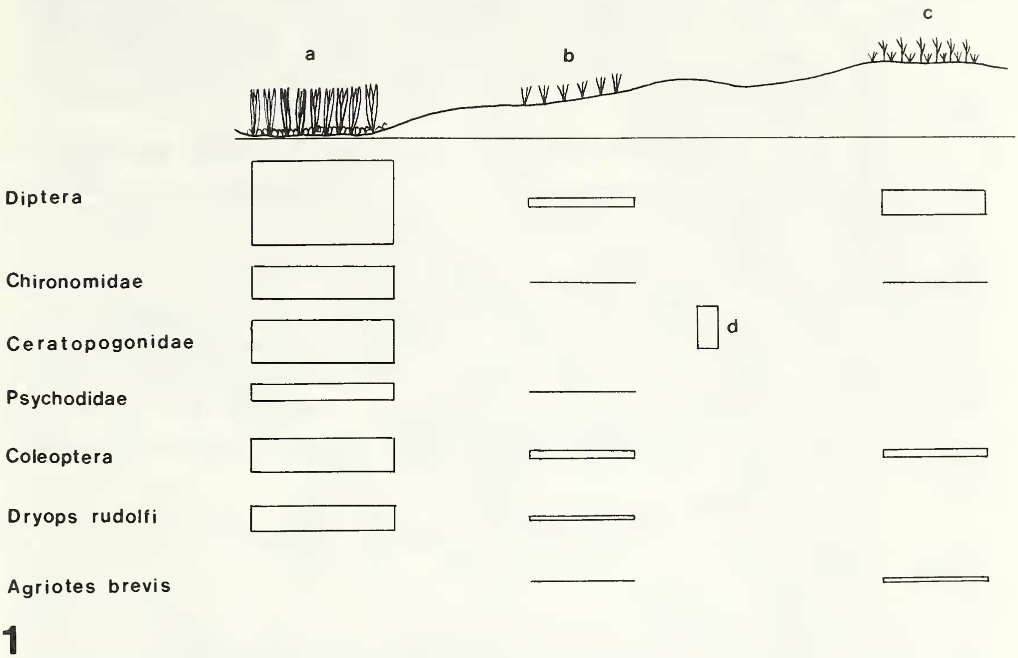

Fig. 1. Distribution of different groups of soil insects in a swampy meadow (a), wet meadow (b) and dry meadow (c) in a periodically inundated area in South Moravia. Height of d - 1000 specimens. m^{-2}. Larvae of some groups of Diptera and *Dryops rudolfi* play an important role in processes that form soil microstructure in the swampy meadow.

To obtain droppings of soil animals known to affect processes of soil formation (gut filled with brown or black particles of dead organic matter in different stages of disintegration and mostly mixed up with mineral particles), immediately after extraction in the Tullgren apparatus the animals are placed into glass jars with wet filter paper on the bottom. It enables us to identify the zoogenous microstructures in soil thin sections with particular species of soil animals. In a further phase, laboratory rearings of the species forming the soil microstructure are carried out to prove their food requirements. In the future we will have enough experience to limit this long procedure to the coenological analysis of particular groups of soil fauna and of other dominant decomposers for which a role in the processes of formation of microstructure are still not established. We may also obtain valuable results by direct observation of soil animals in the field, as is pointed out by Kubiena (1964), Zacharie (1965), Bal (1970) and others. But the importance of many of the soil animals cannot be established by field observation.

SUCCESSION OF SOIL TYPES DURING SUCCESSION OF WHOLE ECOSYSTEMS

The coenological composition of soil fauna and the presence of different groups and species of decomposers in the soil has a crucial effect on the rate and forms of disintegration of dead organic matter. The composition of soil fauna coenoses, together with some other factors, determines what humus form, soil microstructure and soil type will develop in the ecosystem. In my contribution (Rusek, 1978) the connections between successional development of plant communities, soil animal communities and soil types were shown. Soil animals play an active part in the development of soil and whole ecosystems. Soil animal communities are developing and changing during succession, and in association with them the succession of humus forms proceeds as well (Rusek, 1978).

Each soil type has its own, characteristic soil fauna (Fig. 1) a fact which enables us to use soil animals for soil diagnostic purposes (Ghilarov, 1965). It is known that the most developed humus form, the mull, is formed by earthworms. But only some ecological types of earthworms, the endogeic and the anecic ones, form the mull. The epigeic type of earthworms form typical moder. The zoogeographical distribution of earthworms plays an important role in mull distribution. Mull cannot be formed in areas where the aceic and endogeic earthworms are missing; such areas include the Arctic and parts of the boreal zones, as well as initial and little developed soils. In these areas or soil types, only less developed forms of humus (*e.g.*, raw humus, microarthropod moder, arthropod moder, *etc.*) occur. These ecological and zoogeographical rules and dependences in soil and humus development must be kept in mind in evaluating thin sections of soil.

During soil succession many important changes in composition of species and of ecological groups of soil fauna occur. In the first developmental stages usually only microarthropods (Collembola, Acarina) play an important role in processes of formation of soil microstructure, and the microarthropod moder is formed by them. is formed by them. Some soils reach only this developmental stage as a climax. These soils occur most commonly in the Arctic and in the alpine zones. In temperate, subtropic and tropic zones the humus develops to more complex forms, and determination of its micromorphological components is more difficult because of the great diversity of soil animals taking part in its development.

ROLE OF SOIL ANIMALS IN PROCESSES OF FORMATION OF SOIL MICROSTRUCTURE

We may divide processes of soil microstructure formation into three basic categories from the soil zoological point of view:
(a) disintegration of dead organic matter
(b) formation of zoogenic microstructural soil matrix, and
(c) tunnelling and burrowing activities of soil animals.

Disintegration of dead organic matter

The main source of dead organic matter used in processes of formation of the zoogenous soil microstructure is the plant litter. Before disintegration, the litter is intensively invaded by soil microflora and soil microfauna, and only after a certain period is it attacked by larger soil animals and disintegrated step by step. Some species of microarthropods (Collembola, Oribatei) and enchytraeids skeletonize the leaves between the veins only, causing Fensterfrass, whereas larvae of some Mycetophilidae, Lycoridae and other Nematocera also eat the thinner ribs, causing Lochfrass (Figs. 2, 3). Diplopods (*Glomeris* spp., *Julus* spp., *etc.*, Marcyzzi, 1970), isopods and some earthworms bite off larger pieces of leaf tissue together with the thinner ribs. The large midrib of oak leaves is mined by *Rhisotritia minima* (Berlese Oribatei) [after Bal, (1968, *in* Harding and Stuttard, 1974 and Bal, 1970)].

The litter of conifers is disintegrated more slowly and with more difficulty. Parenchymatic tissues are eaten by phthiracarid mites (Oribatei) which leave typical droppings in the bitten

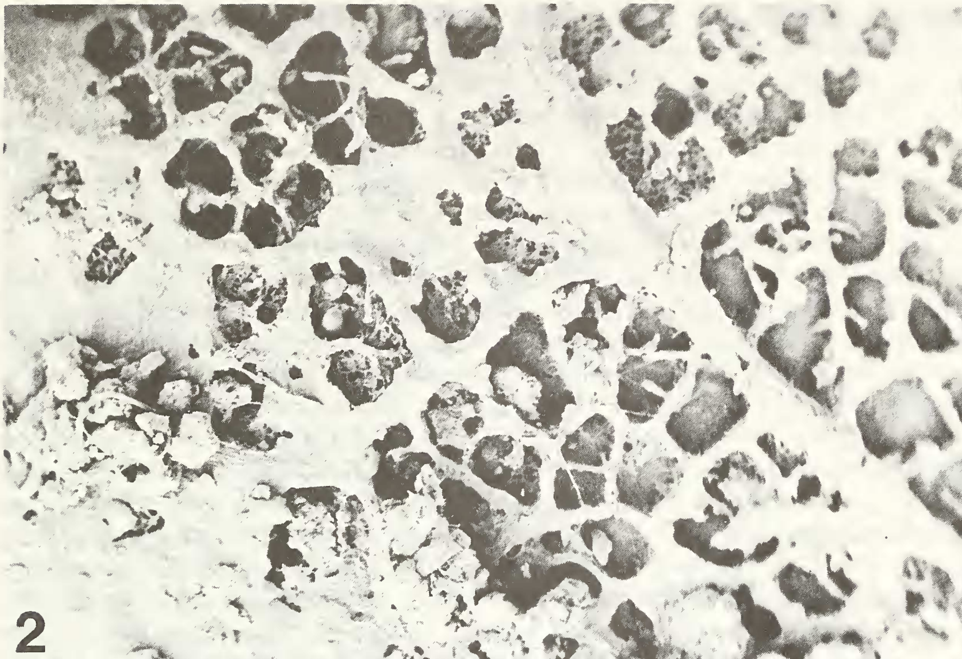

Fig. 2. Oak leaf partly disintegrated by larvae of Mycetophilidae. Their pellets (on the left side) invaded by nematodes.
Fig. 3. Mycetophilid larvae disintegrating leaf litter.

off hollows inside the needles. The needles in the litter layer are also disintegrated by larvae of Tipulidae and Mycetophilidae, caterpillars of *Adela* spp. (Bal, 1970) and by some earthworms (Zachariae, 1966).

Wood disintegration has been studied by many authors, but we only have little data about the zoogenous micromorphological processes in rotting wood (cf. Babel, 1975). Fallen twigs and dead roots are invaded by phthiracarid mites which feed on the rotten wood. In thin sections of soil, we can see large hollows filled by ovoid droppings of these animals (Fig. 4). Often, the periphery of the hollow near the bark is covered by droppings of bark beetles (Scolytidae) secondarily eaten by phthiracarids (Fig. 5). I have observed a few invasions of Collembola (*Mesaphorura* spp.) in the wide, opened hollow of twigs. In such openings, the phthiracarid pellets are mixed with dark Collembolan droppings containing small mineral particles (Fig. 4).

The wood of the tree stumps and logs is disintegrated first by xylophagous larvae and some adults of beetles such as Scolytidae, Curculionidae, Buprestidae and Cerambycidae. When the rotting processes have been advanced, the wood is attacked by larvae of Nematocera (Tipulidae, Mycetophilidae, Lycoridae, *etc.*) and some Lucanidae, Cetoniidae and Dynastidae. The tracks and pellets of these animals are of typical shape, composition and size, but the micromorphological diagnostic characters have not yet been described. After some years a typical soil fauna invades the rotten wood. The pellets of the xylophages are then disintegrated and mixed step by step with mineral particles. Microarthropods, enchytraeids, macroarthropods and some earthworms contribute to this process. In subtropical mountain rain forests in Cuba, larvae and adults of *Passalus* sp. (Coleoptera: Passalidae) play an important role in wood disintegration. After passing through the gut the pieces of wood in the excrement are invaded by special microflora and the droppings are then again eaten by larvae of the same species or other xylophagous animals. In the tunnels of these animals it is easy to distinguish light coloured pellets after the first passage through the gut and the brownish or black ones which passed through two or more times. These droppings then become a food source for a diversified community of soil animals of different size.

Zoogenic formation of the soil matrix microstructure

Through the feeding activity of soil animals, the plant litter is disintegrated and converted into new structures which may be stable or which are further converted by aging or feeding activities of other soil animals, into other microstructures characteristic of the soil matrix. Like the successional development of soil types, the development of humus forms also occurs in successive steps. This successive development has its own regularities connected with the ecology of soil animals from the decomposer ecological group. We may follow the progressive development of humus forms during litter disintegration and during incorporation of the new microstructural elements into the soil matrix. These short term decomposition processes in the humus profile relate to the long term humus form development during succession as does ontogeny to phylogeny in the animal kingdom in Haeckel's biogenetical law. Also this short term development of humus forms in the soil profile has its own regularities which may be observed in, for example, forest soils.

The simplest humus form in xeric succession is the microarthropod moder formed by droppings of Collembola, Oribatei and some small nematoceran-larvae (Diptera) (Rusek, 1978). The next developmental step is the arthropod moder formed mainly by the larger animals belonging to the group of macrofauna (Diplopoda, Isopoda, larvae of Diptera and Coleoptera), by the enchytraeids and by the small epigeic forms of earthworms living in the litter (*e.g., Dendrobaena rubida, Eisenia foetida, etc.*). The arthropod moder is microstructurally heterogenous in comparison with the microarthropod moder. The mull-like moder has more complicated structure. The highest form of humus is mull and it develops only when succession reaches a level at which conditions enable high densities of anecic and endogeic earthworms.

Litter disintegration in a forest soil usually starts with the feeding activity of Collembola, Oribatei and small larvae of Diptera. Their pellets belong to the microarthropod moder and they are readily distinguishable in the uppermost litter layer (Fig. 6). "Later" and deeper in the same litter layer are the larger pellets of enchytraeids, diplopods, larger Diptera larvae, *etc.* belonging to the moder. Microarthropod droppings are also formed in this layer, but they are almost completely comsumed by the macroarthropods and incorporated into their faecal pellets. In some larger pellets they are easily visible in soil thin sections (Fig. 8). The macroarthropod droppings can be secondarily disintegrated by aging into the small, original pellets of microarthropods (Fig. 8). When anecic and endogeic earthworms are present in the soil in high densities, the picture of processes of formation of arthropod moder can be completely obscured by the mull production of these lumbricids. The droppings of macro- and microarthropods are then totally disintegrated and mixed with mineral particles in the guts of these animals (Fig. 7).

The nomenclature of humus forms relates to the whole humus profile; the name of the humus form is derived from the prevailing microstructural elements in the profile. It is difficult to decide what humus form occurs in many samples of certain soil profiles. It is proposed here to identify the humus form in each subhorizon of the L- and F- horizons.

Disintegration of larger droppings by the soil mesofauna (enchytraeids, Collembola, *etc.*) is of great importance in the microstructural forming processes. It is most remarkable in the upper part of the H-horizon, where the large, spongeous droppings of earthworms are eaten by enchytraids and transferred into their small droppings (Zacharie, 1965). The same is true for some Collembola (*e.g., Onychiurus* spp., Tullbergiinae gen. spp.,) (*Folsomia* spp.) (Fig. 8). The macroarthropod droppings in the F-horizon are disintegrated in the same manner as described by Zachariae (1964) for enchytraeids and by Dunger (1983) for Collembola.

Tunnelling and burrowing activities of soil animals

Only soil animals from decomposer ecological groups play a part in the above described disintegration processes. Tunnelling and burrowing are also done by animals from other ecological groups such as herbivores, predators, *etc.* These have usually well sclerotized bodies, strong mandibulae, head capsules and urgomphi, feet adapted to life in soil, well developed muscles, worm-like shapes, *etc.* They aerate the soil profile by their tunnelling activities when moving through the soil in search of food, reproductive or hibernation sites, *etc.* In autumn, the wireworms (Elateridae) injurious to cultivated plants, move 50–60 cm deep to hibernate. They migrate to the soil surface the following spring during which time they make long horizontal channels in the uppermost part of the soil, searching for the roots of the host plants (cf. Rusek, 1972). There is a great diversity of actively tunnelling soil animals within the soil macro- and megafauna, but some species of the soil mesofauna may also make active microtunnels in the soil matrix (*e.g.*, some Collembola from the family Onychiuridae, oribatid mites, enchytraeids). Many of the tunnellers mix the organic matter with mineral particles and translocate the droppings between soil horizons up to the soil surface. During such activities the organic matter may be translocated by earthworms deep into the mineral horizon and the mineral soil components transported to the surface. Soil material is translocated by earthworms, especially

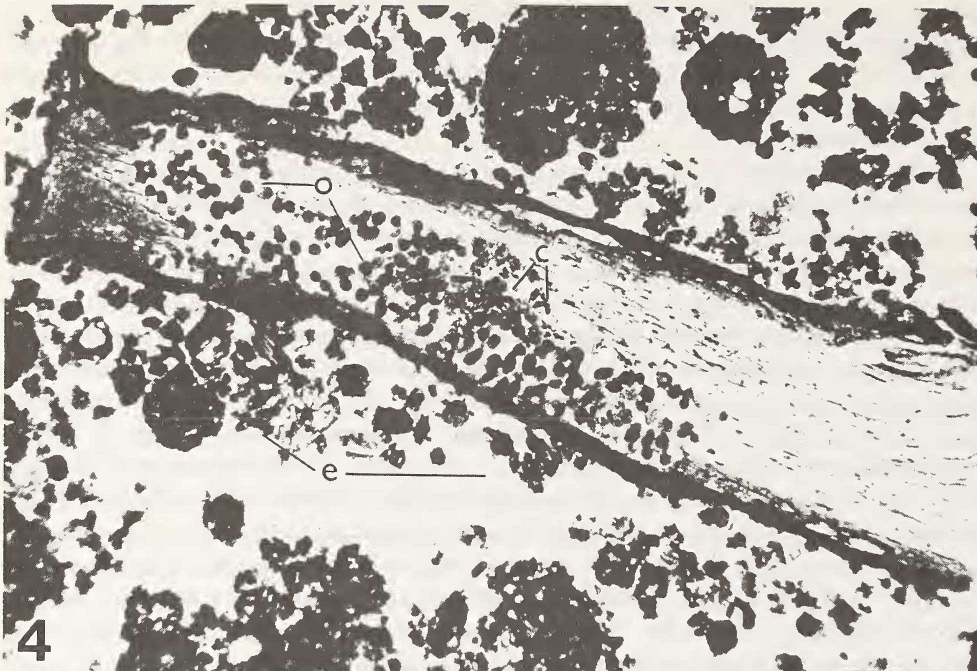

Fig. 4. Soil thin section from a moder rendzina. Pellets of oribatid mites (o) and Collembola (c) inside the small twig, and droppings of enchytraeids (e). Fig. 5. Disintegration of twigs in a moder, by bark beetles and oribatid mites: droppings of these animals are indicated by (s) and (o) respectively.

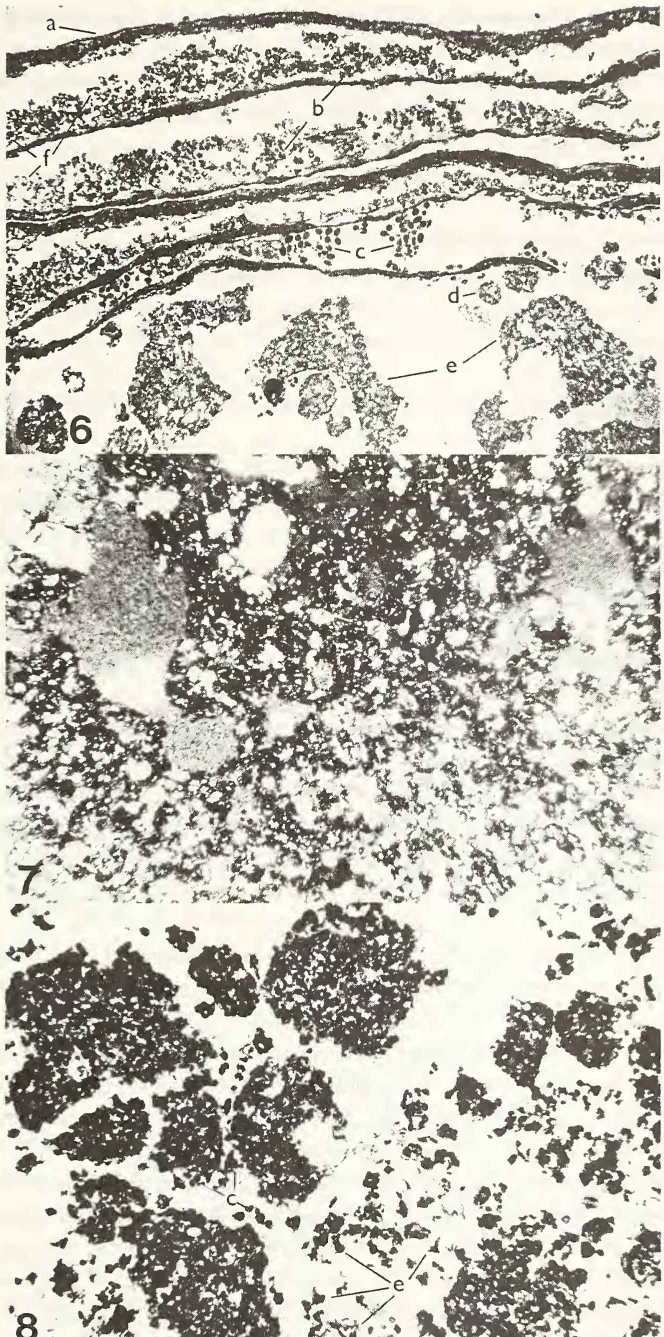

Fig. 6. Oak leaves (a) partly disintegrated by Collembola (f), Enchytraeidae (b), oribatid mites (c). Below the leaves droppings of nematoceran larvae (Diptera) (d) and of the epigeic earthworm *Dendrobaena rubida* (r). Moder rendzina, Bohemian Karst. Fig. 7. Spongeous droppings of an endogeic earthworm, mull. Fig. 8. Droppings of epigeic earthworms subsequently disintegrated by enchytraeids (e) and Collembola (c).

the anecic ones, and also by groups such as ants and some other Hymenoptera, termites dung beetles, some crickets and other insects. The cast-forming activity of anecic earthworms, ants and another animals is well known and of great importance in microstructural and soil forming processes. The zoogenous microstructural cavity system has been analysed in soil thin sections only by a few workers (*e.g.,* Babel and LeNgoc, 1977) and deserves more attention in the future. It is easier to analyse these activities using thick soil sections or on ground block sections than using thin sections of soil.

Because of their macromorphological impact, the burrowing and tunnelling activities of vertebrates were not mentioned in connection with soil microstructure processes. The activities of some groups of the invertebrate soil macro- and megafauna also extend to a macromorphological level during soil succession.

STRUCTURE OF ANIMAL DROPPINGS IN THE SOIL MATRIX

The most important contribution of soil animals to formation of the microstructural fabric is their excrement, also called droppings, pellets or faecal pellets. These are the prevailing primary aggregates of many humus horizons. Each group or even species of soil animal produces droppings of characteristic shape, composition, size and colour (*cf.* Bal, 1973). Location and accumulation within the soil profile are also important features aiding in the determination of the origin of droppings. Some droppings are very stable for a long time, especially in rendzina soils, but usually they change with age or through feeding activities of secondary decomposers. Many taxonomically different groups of soil animals produce similar pellets, which consequently may be misinterpreted in soil thin sections. As was stated in the methodological section, the determination of droppings must start from the coenotical analysis of the soil fauna. The diagnostic features of droppings of the most important soil forming animals groups are described below. The droppings of well known groups as well as groups for which we lack information are described briefly.

Droppings of Oribatei

Pellets of oribatid mites (Oribatei, Acarina) are very distinctive and, in most, are easily recognizable microstructures in the soil matrix. Their characteristics have been described by many authors (*e.g.,* Zachariae, 1965; Bal, 1970; Rusek, 1975): egg-shaped or sphaeric, with smooth surface, very compact and without mineral particles inside, light brown coloured and up to 200 x 140 μm in size, depending on the species and the instar of the mite. Most characteristic are the smooth surface and the missing mineral particles. These two characters are conditioned by the structure of these mites. They have a very narrow pharynx through which mineral particles and larger pieces of food cannot enter the gut (Taraman, 1968). In the ventriculus the ball of food particles is covered by a thick peritrophic membrane (Fig. 9) which also covers the droppings, giving them their smooth surface. Taraman (1968) mentions that the faecal pellets of some oribatid species are grayish or black; their colour may shift from yellow to black during aging, due to the action of microorganisms. The same author notes that pellets of *Steganacarus magnus* fed on wood tissue do not have a smooth surface. These facts may explain why oribatid excrements were not recognized in soil thin sections from places where the macrohumiphagous Oribatei live in high densities.

The oribatid droppings are usually found in groups between the leaves in the L-layer, inside coniferous needles (Fig. 10) or in feeding cavities in rotten wood (Fig. 4). Often groups of droppings of different size are together in one hollow, indicating the moulting cycle of the feeding animal. Macrohumiphagous species from the oribatid family Phthiracaridae are most important in the processes of formation of soil microstructure, but we may also find species in other families contributing to these processes. Oribatid mites occur in all soil horizons.

Droppings of Collembola

Collembola are one of the most abundant representatives of soil mesofauna. They belong together with Acarina and some smaller groups of Tracheata to the group of microarthropods. Quite contradictory data have been published about the importance of Collembola in processes of formation of soil microstructure. Zachariae (1963) is of the opinion that Collembola do not play an important role in the disintegration of organic matter and in the processes of formation of soil microstructure. But previously Kubiena (*e.g.*, 1955) has pointed out the leading role of Collembola in forming some mountain soils (*e.g.*, pitchmoder rendzina). Also Bal (1970), Dunger (1983) and other authors have shown the importance of Collembola in litter disintegration. Kubíková and Rusek (1976) have established that in a xeric protorendzina profile the droppings of Collembola predominate. Rusek (1975) describes the pellets of Collembola, Oribatei and Enchytraeidae and the differences between them.

The droppings of Collembola are usually compact, 30–90 μm in diameter (over 100 μm in larger species), irregularly round, with rugged, irregular surface, usually containing mineral particles, and usually black. The remains of organic matter inside them do not contain larger parts of plant tissue. They clearly differ from the smooth, egg-shaped and light brown oribatid droppings.

Collembola are one of the most ecologically diversified groups of arthropods and this fact has given rise to a lack of understanding of their function in the soil by some authors.

There are Collembola living atmobiotically on higher plants and some of them are even important pests (Fig. 11) (*e.g., Sminthurus viridis*). The epigeic forms are living on the soil surface and in litter and some species are important litter decomposers (*e.g., Tomocerus* spp. (Fig. 12), *Orchesella* spp. (Fig. 13), *Isotoma* spp., *Hypogastrura* spp.). The hemiedaphic species live in the litter and F-horizon, whereas the euedaphic ones are in the F- and H-horizons. Some of the hemiedaphic as well as euedaphic species contribute to the processes of formation of soil microstructure (*e.g., Folsomia* spp., *Onychiurus* spp., *Mesaphorura* spp., *Megalothorax minimus*, *etc.*).

In the Collembola strongly developed feeding specialization exists. We recognize Collembola with sucking mouth parts (*Neanura* spp., *Micranurida* spp., *etc.*), predators (*Friesea* spp., *Cephalotoma grandiceps*), fungivores (*Pseudosinella* spp., *Paratullbergia callipygos*, *etc.*), macrophytophages (*Sminthurus* spp., *Bourletiella* spp. (Fig. 11), *etc.*), detritivores and other specialists. It is no wonder that any one who observed a phytophagous or microhumiphagous species arrives at wrong conclusions about the roles of Collembola in soil forming processes.

I am not implying that all species of Collembola play a role in soil formation. The same situation occurs in almost all groups of soil arthropods, and we must always distinguish ecological groups.

As already mentioned, the Collembola have a leading role in forming the soil microstructure in some arctic, alpine and weakly developed soils. Sometime the whole soil profile of these soils is formed primarily by collembolan droppings (Fig. 14). In more developed soils Collembola take part in disintegration of leaf litter (Fig. 6) and in secondary disintegration of macro- and

Fig. 9. *Hypochtonius* sp. (Oribatei), v-ventriculus; p-peritrophic membrane with a ball of food particles inside. Semi-thin section prepared by Smrž. Fig. 10. *Abies alba* needles disintegrated inside by phthiracarid mites (Oribatei). Their pellets are of typical shape (o). Fig. 11. *Bourletiella lutea* (Collembola) feeding on living plant tissues does not contribute to the soil microstructures.

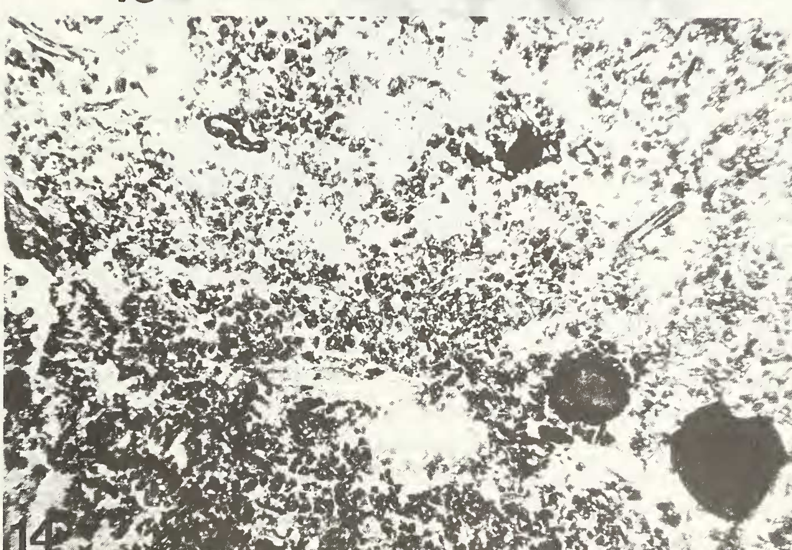

Fig. 12. *Tomocerus minor*, an epigeic species of Collembola.– Feeding on the leaves in the L-layer contributes to the soil microstructures by its small cylindrical pellets (a group of them on the right side). Fig. 13. *Orchesella cincta* (Collembola) takes part in leaf litter disintegration. Fig. 14. Pellets of Collembola predominate in some alpine soil types. Schneetälchen rendzina, West Tatra mountains.

megafauna droppings (Fig. 8). The small collembolan pellets can be found in lumbricid channels, as well as inside their large, spongeous excrements in which the Collembola bite narrow hollows and channels. Collembolan droppings are often confused with pellets of enchytraeids.

Droppings of Enchytraeidae

The enchytraeids are intermediate in body length between the soil mesofauna and macrofauna. In the size of their excrements, they are close to the mesofauna. The droppings are described in many papers (*e.g.*, Zachariae, 1964; Babel, 1968; Rusek, 1975). The pellets of some enchytraeid species resemble those of Collembola; in other species, they differ distinctly from the collembolan ones in their shape, size, and arrangement and location in the soil profile. They are the leading microstructural components in some soils (Babel, 1968). In the lower L-layer, the enchytraeid pellets are often in two parallel rows, forming channels between the leaves (Zachariae, 1964). In the F- and H-horizons enchytraeids are secondary decomposers of the larger excrements of soil macrofauna (Fig. 8). They make narrow channels in the large, spongeous earthworm excrements (Zachariae, 1964).

The enchytraeid droppings are 120–200 μm long, of extremely irregular shape, and with irregular surface. They contain mineral particles and pieces of plant tissues and many are divided into primary components (pellets of microarthropods, plant and mineral particles). In the deeper soil horizons most contain mineral particles larger than the collembolan pellets, and the collembolan pellets are smaller than are those of the enchytraeids.

Droppings of Diptera, Coleoptera and larvae of other insects

Larvae of Diptera belong partly to the soil mesofauna (Lycoridae, Mycetophilidae, Chironomidae *etc.*, and partly to the macrofauna (Tipulidae, Bibionidae, *etc.*). Most form sphaerical, cylindrical or spindle-like droppings belonging to the moder humus form. They contain large pieces of plant tissues mixed sparsely with mineral particles, which may sometimes be missing. Their length ranges from 100 μm to 1 mm (Bibionidae, Lycoridae, Mycoridae, Mycetophilidae, and even more (Tipulidae). The droppings of Bibionidae are well described by Szabo *et al.* (1967). They contain leaf residues, some algal filaments, structureless organic substances and mineral particles, and they reach 0.3 to 0.4 mm in diameter and are up to 1 mm long. The droppings of Tipulidae larvae (Fig. 15) are egg-shaped and contain large pieces of plant material mixed in many cases with large mineral particles. Their surface is covered by a peritrophic membrane. They are concentrated in the litter layer and some species also are in the uppermost H-horizon. The droppings of litter feeding mycetophilid larvae are concentrated in the L-layer. They are sphaerical and contain small pieces of leaf tissues, 70–200 μm in diameter and are not very stable.

Also some larvae of Coleoptera contribute to the soil microstructures. Droppings of some groups are sphaerical, some more than 5 mm in diameter (*Melolontha* spp.); others resemble large droppings of Enchytraeidae, *e.g.*, those of *Dryops rudolfi* (Figs. 16, 17). The droppings of the last species are an important part of the microstructure in the temporarily inundated soils in South Moravia (Rusek, 1973, 1984).

Bal (1970) described droppings of *Adela* sp. caterpillars disintegrating conferous needles. They are cylindrical, solid, often contracted in the middle, with pieces of plant tissues. Their size reaches 510 x 260 μm and they are deposited in small groups.

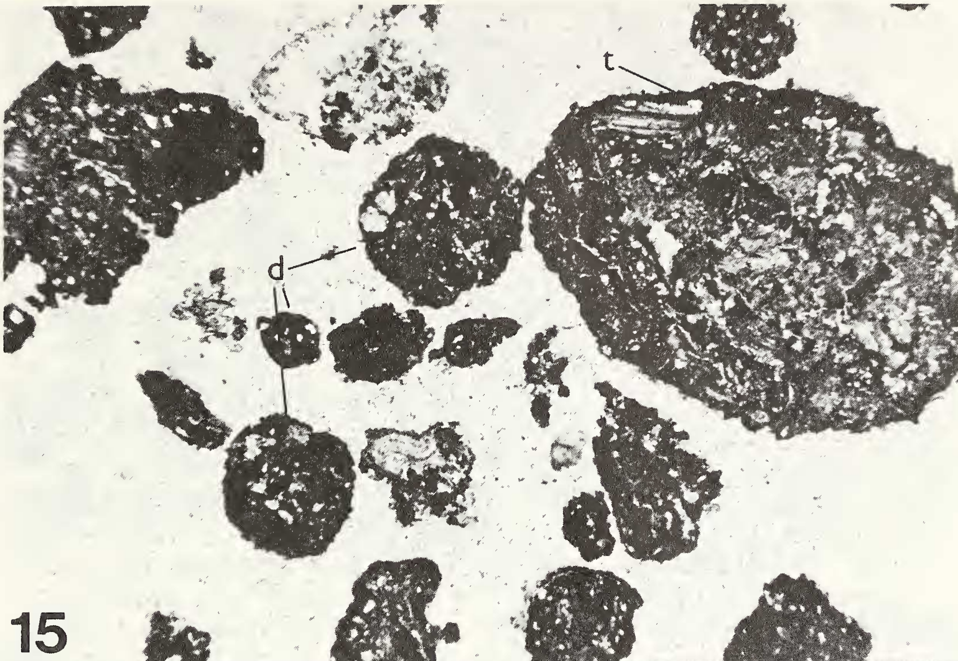

Fig. 15. Diplopod (d) and tipulid (t) larvae pellets in a moder rendzina in Bohemian Karst. Fig. 16. *Dryops rudolfi* larva (Coleoptera: Dryopidae) from a periodically flooded swampy meadow in south Moravia. Gut filled with black particles of dead organic matter and mineral particles.

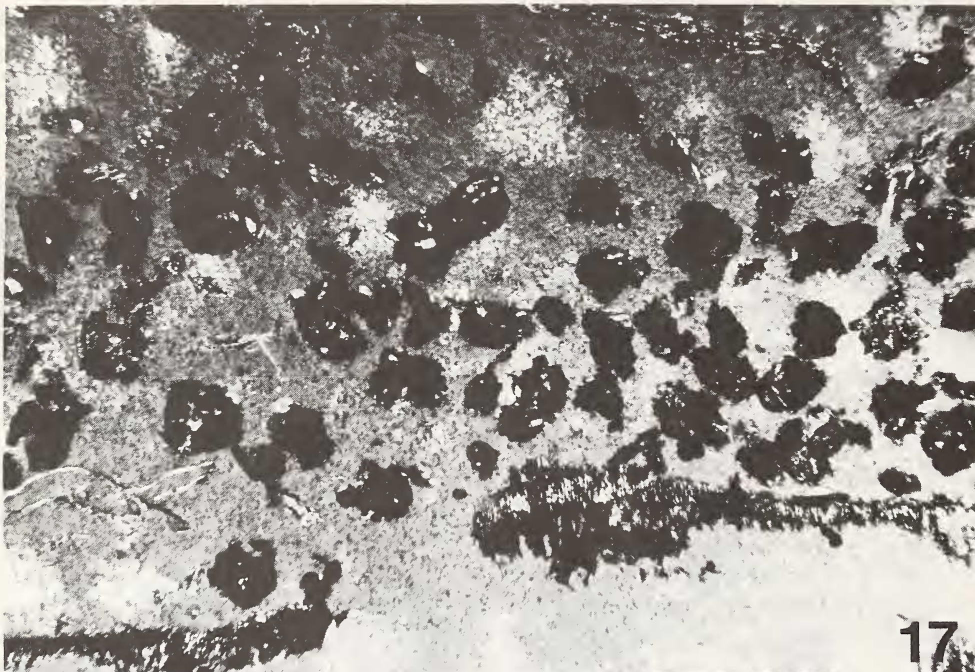

Fig. 17. Droppings of *Dryops rudolfi* larvae with residue of disintegrated leaves of *Glyceria maxima* in L-layer. Fig. 18. Droppings of diplopods (a) in a mull-like moder rendzina in Bohemian Karst.

Droppings of Diplopoda and Isopoda

The droppings of litter-consuming diplopods are characteristic microstructural elements in many soil types. They are, for example, the dominant droppings in moder rendzina and in the upper part of mull-like rendzina (Kubíková and Rusek, 1976). The diplopod droppings range in size from 0.5 to 4 mm. Many contain large pieces of litter fragments, droppings of smaller soil animals and many also a great quantity of mineral particles. The internal structure is not very compact (Fig. 18). In most species, the droppings are covered with a peritrophic membrane. The droppings of large julids and glomerids are egg-shaped or sphaerical; those of small julids are elongate (Babel, 1975).

Droppings of isopods, which also consume litter are very similar. These droppings are relatively rare in thin sections of soil due to the special ecological requirements of most isopod species. The animals may be slightly more abundant in very small specific areas. The size and internal structure of their pellets is almost the same as in diplopods. They are cylindrical and some have a longitudinal cleft.

Droppings of Lumbricidae

The microstructures of lumbricid droppings are well known, and they are described in almost all contributions dealing with the role of soil fauna in the formation of soil microstructure (*e.g.,* Kubiena, 1958; Zachariae, 1965; Babel, 1975). The structure, size and internal composition of lumbricid droppings depend on the ecological group which produces them. The epigeic forms produce microstructures belonging to the moder form of humus, the endogeic and anecic ones produce mull-like or mull excrements. The epigeic group usually produces cylindrical or irregular droppings containing plant material of different stages of degradation (brown to black in colour) mixed with some mineral particles (*Dendrobaena rubida*, *Eisenia foetida*, *Eisenia lucens*, *etc.*) (Fig. 6). The droppings of endogeic and anecic groups are spongeous, with very small pieces of organic matter well mixed with a great quantity of mineral particles of variable size (Fig. 7). Most of these droppings are usually subsequently disintegrated by the mesofauna (Fig. 8). They may occupy the whole humus horizon and the upper parts of the mineral horizon, and within lumbricid channels they may extend deep into the C-horizon.

REFERENCES

Babel, U. 1968. Enchytraeen-Losungsgefüge im Löss. Geoderma, 2: 37–63.

Babel, U. 1975. Micromorphology of soil organic mattter. pp. 369–473. *In*: Gieseking J.E. (Editor). Soil Components. Volume 1. Organic Components. Springer Verlag, New York, Heidelberg, Berlin.

Babel, U. and B. LeNgoc. 1977. Regradierung von Mergelböden nach Schafweidenutzung. Mitt. Dtsch. Bodenkundl. Gesellsch., 25: 313–320.

Bal, L. 1970. Morphological investigation in two moderhumus profiles and the role of the soil fauna in their genesis. Geoderma, 4: 5–35.

Bal, L. 1973. Micromorphological analysis of soils. Lower levels in the organization of organic soil materials. Soil Surv. Inst., Wageningen, 174 pp.

Dunger, W. 1983. Tiere im Boden. Die Neue Brehm-Bücherei. A. Ziemsen Verlag-Wittenberg Lutherstadt, 280 pp.

Ghilarov, M.S. 1965. Zoological methods in soil diagnostics. Publ. Office "Nauka". Moscow,

279 pp.
Harding, D.J.L. and R.A. Stuttard. 1974. Microarthropods, pp. 489–532. *In*: Dickinson, C.H. and G.J.F. Pugh (Editors). Biology of plant litter decomposition. Academic press, London and New York, Volume 2.
Jongerius, A. (Editor). 1964: Soil micromorphology. Elsevier, Amsterdam, 540 pp.
Kubiena, W.L. 1943. L'investigation microscopique de l'humus. Z. Weltforschirt., 10: 387–410.
Kubiena, W.L. 1948. Entwicklungslehre des Bodens. Springer-Verlag, Wien.
Kubiena, W.L. 1955. Animal activity in soils as a decisive factor in establishment of humus forms, pp. 73–82. *In*: Kevan, D.K.McE. (Editor). Soil zoology. Butterworths Sci. Publ., London.
Kubiena, W.L. 1964. The role and mission of micromorphology and microscopic biology in modern soil science, pp. 1–13. *In*: Jongerius, A. (Editor). Soil micromorphology. Elsevier, Amsterdam.
Kubíková, J. and J. Rusek. 1976. Development of xerothermic rendzinas. A study in ecology and soil microstructure. Rozpravy ČSAV, Academia, Praha, 79 pp. + 16 plts.
Marcuzzi, G. 1970. Experimental observation on the role of *Glomeris* spp. (Myriapoda Diplopoda) in the process of humification of litter. Pedobiol. 10: 401–406.
Rusek, J. 1972. Die mitteleuropäischen Agriotes- und Ectinus- Arten (Coleoptera, Elateridae), mit besonderer Berücksichtigung von A. brevis un den in Feldkulturen lebenden Arten. Rozpravy Českosl. akad. věd, Academia, Praha. 90 pp. + 3 Tab.
Rusek, J. 1973. *Dryops rudolfi* sp.n. und seine Larve (Coleoptera, Dryopidae). Acta Ent. Bohemoslov., 70: 86–97.
Rusek, J. 1975. Diebodenbildende Funktion von Collembolen und Acarina. Pedobiologia, 15: 299–308.
Rusek, J. 1978. Pedozootische Sukzessionen während der Entwicklung von Ökosystemen. Pedobiologia, 18: 426–433.
Rusek, J. 1984. Zur Bodenfauna in drei Typen von Überschwemmungswiesen in Süd-Mähren. Rozpravy ČSAV, Academia Praha, 128 pp. + 8 tbls.
Szabo, J., T. Bartlay, and M. Marton. 1967. The role and importance of the larvae of St. Mark's fly in the formation of a rendzina soil, pp. 475–489. *In*: Graft, O. and J.E. Stachell. (Editors). Progress in Soil biology. Braunschweig and Amsterdam.
Taraman, K. 1968. Anatomy, histology of oribatid gut and their digestion. Biološki Vestnik, 16: 67–76.
Zachariae, G. 1963. Was leisten Collembolen für den Waldhumus? pp. 109–124. *In*: Doeksen, J. and J. van der Drift. (Editors). Soil organisms. North Holland Publishing Comp., Amsterdam.
Zachariae, G. 1964. Welche Bedeutung haben Enchytraeen im Waldboden? pp. 57–68. *In*: Jongerius, A. Soil micromorphology. Elsevier Publ. Comp., Amsterdam.
Zachariae, G. 1965. Spuren tierischer Tätigkeit im Boden des Buchenwaldes. Forstwiss. Forschungen. Heft 20: 1–68.
Zachariae, G. 1966. Die Streuzersetzung im Kohlgartengeibiet, pp. 490–506. *In*: Graft, O. and J.E. Satchell. (Editors). Progress in Soil biology. Braunschweig and Amsterdam.